Title: Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest

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Summary

- As climate change drives increased drought in many forested regions, mechanistic understanding of the factors conferring drought tolerance in trees is increasingly important. The dendrochronological record provides a window through which we can understand how tree size and traits shape growth responses to droughts.

- We analyzed tree-ring records for twelve species in a broadleaf deciduous forest in Virginia (USA) to test hypotheses on how tree height, microenvironment characteristics, and species' traits shaped drought responses across the three strongest regional droughts over a 60-year period.

- Drought tolerance (resistance, recovery, and resilience) decreased with tree height, which was strongly correlated with exposure to higher evaporative demand and solar radiation. The potentially greater rooting volume of larger trees did not confer a resistance advantage, but marginally increased recovery and resilience, in sites with low topographic wetness index. Drought tolerance was greater among species whose leaves experienced less shrinkage upon desiccation and lost turgor (wilted) at more negative water potentials.

- The tree-ring record reveals that tree height and leaf drought tolerance traits influenced growth responses during and after significant droughts in the meteorological record. As climate change-induced droughts intensify, tall trees with drought-sensitive leaves will be most vulnerable to immediate and longer-term growth reductions.

Key words: annual growth; crown exposure; drought; Forest Global Earth Observatory (ForestGEO); leaf drought tolerance traits; temperate broadleaf deciduous forest; tree height; tree-ring

Introduction

Forests play a critical global role in climate regulation (Bonan, 2008), yet there remains enormous uncertainty as to how the forest-dominated terrestrial carbon sink will respond to climate change (Friedlingstein et al., 2006). An important aspect of this uncertainty lies with physiological responses of trees to drought (Kennedy et al., 2019). In many forested regions around the world, the risk of severe drought is increasing (Trenberth et al., 2014; Dai et al., 2018), often despite increasing precipitation (Intergovernmental Panel on Climate Change, 2015; Cook et al., 2015). Droughts, intensified by climate change, have been affecting forests worldwide and are expected to continue as one of the most important drivers of forest change in the future (Allen et al., 2010, 2015; McDowell et al., 2020). Understanding forest responses to drought requires elucidation of how tree size, microenvironment, and species' traits jointly influence individual-level drought tolerance, defined here as a tree's ability to maintain growth during drought (resistance) and to recover to its pre-drought growth rate (resilience) (Lloret et al., 2011). Because the resistance and resilience of growth to drought are linked to trees' probability of surviving drought (DeSoto et al., 2020; Liu et al., 2019), understanding growth responses can also help elucidate which trees are most vulnerable to drought-induced mortality. However, it has proven difficult to resolve the many factors affecting tree growth during drought and the extent to which their influence is consistent across droughts. This is because available forest census data only rarely captures extreme drought, whereas tree-ring records capture multiple droughts but typically focus on only the largest individuals of one or a few species.

Many studies have shown that within and across species, large trees tend to be more affected by drought. Greater growth reductions (*i.e.*, lower drought resistance) in larger trees were first shown on a global scale by Bennett et al. (2015), and subsequent studies have reinforced this finding (*e.g.*, Gillerot et al., 2020). Although lower recovery and resilience of larger trees have also been observed (Hacket-Pain et al., 2016; Gillerot et al., 2020), in general we have much more limited understanding of how and why these scale with tree size.

physiological model of Trugman et al. (2018) predicts that recovery and resilience would not necessarily be lower, even in trees that will ultimately die.

Moreover, it has yet to be resolved which of several potential underlying mechanisms most strongly shape these trends in drought response. First, tree height itself may be a primary driver. Taller trees face the biophysical challenge of lifting water greater distances against the effects of gravity and friction (McDowell et al., 2011; McDowell and Allen, 2015; Ryan et al., 2006; Couvreur et al., 2018). Vertical gradients in stem and leaf traits–including smaller and thicker leaves (higher leaf mass per area, LMA), greater resistance to hydraulic dysfunction (*i.e.*, more negative water potential at 50% loss of hydraulic conductivity, more negative P50), and lower hydraulic conductivity at greater heights (Couvreur et al., 2018; Koike et al., 2001; McDowell et al., 2011)–enable trees to become tall (Couvreur et al., 2018). Greater stem capacitance (*i.e.*, water storage capacity) of larger trees may also confer resistance to transient droughts (Phillips et al., 2003; Scholz et al., 2011). Taller trees have wider conduits in the basal portions of taller trees, both within and across species (Olson et al., 2018; Liu et al., 2019) and throughout the conductive systems of angiosperms (Zach et al., 2010; Olson et al., 2014, 2018), which help maintain constant the resistance that would otherwise increase as trees grow taller. Wider xylem conduits plausibly make large trees more vulnerable to embolism during drought (Olson et al., 2018), and traits conducive to efficient water transport may also lead to poor ability to recover from or re-route water around embolisms (Roskilly et al., 2019). **(here would be a good place to comment on resilience. "What may help the tree in competition, therefore,**

84 **can also be a deteriment to drought resilience.")**

85 Larger trees may also have lower drought tolerance because of microenvironmental and ecological factors.
86 Their crowns tend to occupy more exposed canopy positions, which are associated with higher evaporative
87 demand (Kunert et al., 2017). Subcanopy trees tend to fare better specifically due to the benefits of a
88 buffered environment (Pretzsch et al., 2018). Counteracting the liabilities associated with tall height, large
89 trees tend to have larger root systems (Enquist and Niklas, 2002; Hui et al., 2014), potentially mitigating
90 some of the biophysical challenges they face by allowing greater access to water. Larger root systems–if they
91 grant access to deeper water sources–would be particularly advantageous in drier microenvironments (e.g.,
92 hilltops, as compared to valleys and streambeds) during drought. Finally, tree size-related responses to
93 drought can be modified by species' traits and their distribution across size classes (Meakem et al., 2018; Liu
94 et al., 2019). Understanding the mechanisms driving the greater relative growth reductions of larger trees
95 during drought requires sorting out the interactive effects of height and associated exposure, root water
96 access, and species' traits.

97 Debates have also arisen regarding the traits influencing tree growth responses to drought. Studies within
98 temperate broadleaf forests have observed ring-porous species showing higher drought tolerance than
99 diffuse-porous species (Friedrichs et al., 2009; Elliott et al., 2015; Kannenberg et al., 2019), but this
100 distinction does not always hold (Martin-Benito and Pederson, 2015), would not hold in the global context
101 (Wheeler et al., 2007; Olson et al., 2020) and does not resolve differences among the many species within
102 each category. Commonly-measured traits including wood density and leaf mass per area (LMA) have been
103 linked to drought responses within some temperate deciduous forests (Abrams, 1990; Guerfel et al., 2009;
104 Hoffmann et al., 2011; Martin-Benito and Pederson, 2015) and across forests worldwide (Greenwood et al.,
105 2017). However, in other cases these traits could not explain drought tolerance (e.g., in a tropical rainforest;
106 Maréchaux et al., 2019), or the direction of response was not always consistent. For instance, higher wood
107 density has been associated with greater drought resistance at a global scale (Greenwood et al., 2017), but
108 correlated negatively with tree performance during drought in a broadleaf deciduous forest in the
109 southeastern United States (Hoffmann et al., 2011). Thus, the perceived influence of these traits on drought
110 resistance may actually reflect indirect correlations with other traits that more directly drive drought
111 responses (Hoffmann et al., 2011).

112 In contrast, hydraulic traits have direct physiological linkages to tree growth and mortality responses to
113 drought. For instance, water potentials at which percent the loss of conductivity surpasses a certain
114 threshold (e.g., P50 and P88, representing 50 and 88% loss of conductivity, respectively) and hydraulic safety
115 margin (*i.e.*, difference between typical minimum water potentials and P50 or P88) correlate with drought
116 performance across global forests (Anderegg et al., 2016). However, these are time-consuming to measure and
117 therefore infeasible for predicting or modeling drought responses in highly diverse forests (*e.g.*, in the tropics).
118 More easily-measurable leaf drought tolerance traits that have direct linkage to plant hydraulic function can
119 explain variation in plant distribution and function (Medeiros et al., 2019). These include leaf area shrinkage
120 upon desiccation (PLA_{dry}; Scoffoni et al., 2014) and the leaf water potential at turgor loss point (π_{tlp}), *i.e.,*
121 the water potential at which leaf wilting occurs (Bartlett et al., 2016a; Zhu et al., 2018). Both traits correlate
122 with hydraulic vulnerability and drought tolerance as part of unified plant hydraulic systems (Scoffoni et al.,
123 2014; Bartlett et al., 2016a; Zhu et al., 2018; Farrell et al., 2017). The abilities of both PLA_{dry} and π_{tlp} to
124 explain the drought tolerance of tree growth remains untested.

125 Here, we examine how tree height, microenvironment characteristics, and species' traits collectively shape

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126 three metrics of drought tolerance: (1) resistance, defined as the ratio of annual stem growth in a drought
127 year to that which would be expected in the absence of drought based on previous years' growth; (2)
128 recovery, defined the ratio of post-drought growth to growth during the drought year; and (3) resilience,
129 defined as the ratio of post-drought to pre-drought growth (Lloret et al., 2011). We test a series of
130 hypotheses and associated specific predictions (Table 1) based on the combination of tree-ring records from
131 the three strongest droughts over a 60-year period (1950 - 2009), species trait measurements, and census and
132 microenvironmental data from a large forest dynamics plot in Virginia, USA. First, we focus on how tree size,
133 alone and in its interaction with microenvironmental gradients, influences drought tolerance. We examine the
134 contemporary relationship between tree height and microenvironment, including growing season
135 meteorological conditions and crown exposure. We then test whether, consistent with most forests globally,
136 larger-diameter, taller trees tend to have lower drought tolerance in this forest, which is in a region (eastern
137 North America) represented by only two studies in the global review of (Bennett et al., 2015). We also test
138 for an influence of potential access to available soil water, which should be greater for larger trees in dry but
139 not in perpetually wet microsites. Finally, we focus on the role of species' traits, testing the hypothesis that
140 species' traits--particularly leaf drought tolerance traits--predict drought tolerance. We test predictions that
141 drought tolerance is higher in ring-porous than semi-ring and diffuse-porous species and that it is correlated
142 with wood density–either positively (Greenwood et al., 2017) or negatively (Hoffmann et al., 2011) and
143 positively correlated with LMA. We further test predictions that species with low PLA_{dry} and those whose
144 leaves lose turgor at lower water potentials (more negative π_{tlp}) have higher tolerance.

Materials and Methods

Study site and microclimate

147 Research was conducted at the 25.6-ha ForestGEO (Forest Global Earth Observatory) study plot at the
148 Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78°08'43.4"W; Fig. **S1**)
149 (Bourg et al., 2013; Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains
150 near the northern boundary of Shenandoah National Park. Elevations range from 273 to 338 m above sea
151 level with a topographic relief of 65m (Bourg et al., 2013). Climate is humid temperate, with mean annual
152 temperature of 12.7°C and precipitation of 1005 mm yr^{-1} during our study period (1960-2009; source: CRU
153 TS v.4.01; Harris et al., 2014). Dominant tree taxa within this secondary forest include *Liriodendron*
154 *tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.; Table 2).

Identifying drought years

156 We identified the three largest droughts within the time period 1950-2009, defining drought (Slette et al.,
157 2019) as events with anomalously dry peak growing season climatic conditions. Specifically, we used the
158 metric of Palmer Drought Severity Index (PDSI) during May-August (MJJA; Table S1), which were
159 identified by Helcoski et al. (2019) as the months of the current year to which annual tree growth was most
160 sensitive at this site. PDSI divisional data for Northern Virginia were obtained from NOAA
161 (https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp) in December 2017. Based on this, we
162 identified the three strongest droughts during the study period (Figs. **1, S1**; Table S1).

163 The droughts differed in intensity and antecedent moisture conditions (Fig. **S1**, Table S1). The 1966 drought
164 was preceded by two years of moderate drought during the growing season and severe to extreme drought
165 starting the previous fall. In August 1966, $PDSI$ reached its lowest monthly value (-4.82) of the three

166 droughts. The 1977 drought was the least intense throughout the growing season, and it was preceded by 2.5
167 years of near-normal conditions, making it the mildest of the three droughts. The 1999 drought was preceded
168 by wetter than average conditions until the previous June, but $PDSI$ plummeted below -3.0 in October 1998
169 and remained below this threshold through August 1999. Following all three droughts, $PDSI$ rebounded to
170 near-normal conditions in September or October (Fig. **S1**).

171 *Data collection and preparation*

172 Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree heights,
173 microenvironment characteristics, and species traits (Table 3). The SCBI ForestGEO plot was censused in
174 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems ≥ 1cm
175 diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit,
176 1998). From these census data, we used measurements of DBH from 2008 to calculate historical DBH and
177 data for all stems ≥ 10cm to analyze functional trait composition relative to tree height (all analyses
178 described below). Census data are available through the ForestGEO data portal (www.forestgeo.si.edu).

179 We analyzed tree-ring data (xylem growth increment) from 571 trees representing the twelve dominant
180 species (Table 2; Fig. **S2**). Selected species were those with the greatest contributions to woody aboveground
181 net primary productivity ($ANPP_{stem}$) and together comprised 97% of study plot $ANPP_{stem}$ between 2008
182 and 2013 (Helcoski et al., 2019). Cores (one per tree) were collected within the ForestGEO plot at breast
183 height (1.3m) in 2010-2011 or 2016-2017. In 2010-2011, cores were collected from randomly selected live trees
184 of each species that had at least 30 individuals ≥ 10 cm DBH (Bourg et al., 2013). Annual tree mortality
185 censuses were initiated in 2014 (Gonzalez-Akre et al., 2016), and in 2016-2017, cores were collected from all
186 trees found to have died since the previous year's census. We note that drought was probably not a cause of
187 mortality for these trees, as monthly May-Aug $PDSI$ did not drop below -1.75 in these years or the three
188 years prior (2013-2017), and that trees cored dead displayed similar climate sensitivity to trees cored live
189 (Helcoski et al., 2019). Lagged drought-induced mortality would be unlikely, given that the trees analyzed
190 here lived at least 17-18 years past the most recent major drought (1999), whereas the meta-analysis of
191 Trugman et al. (2018) indicates that >10-year lags in drought-attributed mortality are rare. Cores were
192 sanded, measured, and crossdated using standard procedures, as detailed in (Helcoski et al., 2019). The
193 resulting chronologies (Fig. **1a**) were published in Zenodo (Gonzalez-Akre et al., 2019).

194 For each cored tree, we combined tree-ring records and allometric equations of bark thickness to reconstruct
195 DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

$$DBH_Y = DBH_{2008} - 2 * \left[r_{bark,2008} - r_{bark,Y} + \sum_{year=Y}^{2008} r_{ring,Y} \right]$$

196 Here, Y denotes the year of interest, r_{ring} denotes ring width derived from cores, and r_{bark} denotes bark
197 thickness, which was estimated from species-specific allometries based on the bark thickness data from the
198 site (Table S2; Anderson-Teixeira et al., 2015b).

199 Tree heights (H) were measured by several researchers for a variety of purposes between 2012 and 2019
200 (n=1,518 trees). Methods included direct measurements using a collapsible measurement rod on small trees
201 (NEON, 2018) or a tape measure on recently fallen trees (this study); geometric calculations using clinometer
202 and tape measure (Stovall et al., 2018a) or digital rangefinders (Anderson-Teixeira et al., 2015b; NEON,

2018); and ground-based LiDAR (Stovall et al., 2018b). Rangefinders used either the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. Both methods are associated with some error (Larjavaara and Muller-Landau, 2013), but in this instance there was no clear advantage of one or the other. Measurements from the National Ecological Observatory Network (NEON) were collected near the ForestGEO plot following standard NEON protocol, whereby vegetation of short stature was measured with a collapsible measurement rod, and taller trees with a rangefinder (NEON, 2018). Species-specific height allometries were developed using log-log regression ($ln[H] \sim ln[DBH]$; Table S3). For species with insufficient height data to create reliable species-specific allometries (n=2, JUNI and FRAM), heights were calculated from an equation developed by combining the height measurements across all species. We then used these allometries to estimate H for each drought year, Y, based on reconstructed DBH_Y (Fig. **S3**).

To characterize how environmental conditions vary with height, data were obtained from the NEON tower located <1km from the study area via the neonUtilities package (Lunch et al., 2020). We used wind speed, relative humidity, and air temperature data, all measured over a vertical profile spanning heights from 7.2 m to above the top of the tree canopy (31.0 or 51.8m, depending on censor), for the years 2016-2018 (NEON, 2018). After filtering for missing and outlier values, we determined the daily minima and maxima, which we then aggregated at the monthly scale.

Crown position–a categorical variable classifying trees based on exposure to sunlight–was recorded for all cored trees that remained standing during the growing season of 2018 following the protocol of Jennings et al. (1999). Trees were classified as follows: *dominant* trees were defined as those with crowns above the general level of the canopy, *co-dominant* trees as those with crowns within the the canopy; *intermediate* trees as those with crowns below the canopy level, but illuminated from above; and *suppressed* as those below the canopy and receiving minimal direct illumination from above.

Topographic wetness index (TWI), used here as a metric of long-term mean moisture availability, was calculated using the dynatopmodel package in R (Fig. **S2**) (Metcalfe et al., 2018). Originally developed by Beven and Kirkby (1979), TWI was part of a hydrological run-off model and has since been used for a number of purposes in hydrology and ecology (Sørensen et al., 2006). TWI calculation depends on an input of a digital elevation model (DEM; ~3.7 m resolution from the elevatr package (Hollister, 2018)), and from this yields a quantitative assessment defined by how "wet" an area is, based on areas where run-off is more likely. From our observations in the plot, TWI performed better at categorizing wet areas than the Euclidean distance from the stream.

Species' trait data were collected in August 2018 (Tables 2-3; Fig. **S4**). We sampled small, sun-exposed branches up to eight meters above the ground from three individuals of each species in and around the ForestGEO plot. Sampled branches were re-cut under water at least two nodes above the original cut and re-hydrated overnight in covered buckets under opaque plastic bags before measurements were taken. Rehydrated leaves taken towards the apical end of the branch (n=3 per individual: small, medium, and large) were scanned, weighed, dried at 60° C for $\geq$ 48 hours, and then re-scanned and weighed. Leaf area was calculated from scanned images using the LeafArea R package (Katabuchi, 2019). LMA was calculated as the ratio of leaf dry mass to fresh area. PLA_{dry} was calculated as the percent loss of area between fresh and dry leaves. Wood density was calculated for ~1cm diameter stem samples (bark and pith removed) as the ratio of dry weight to fresh volume, which was estimated using Archimedes' displacement. We used the rapid determination method of Bartlett et al. (2012) to estimate osmotic potential at turgor loss point (π_{tlp}).

245 Briefly, two 4 mm diameter leaf discs were cut from each leaf, tightly wrapped in foil, submerged in liquid

246 nitrogen, perforated 10-15 times with a dissection needle, and then measured using a vapor pressure

247 osmometer (VAPRO 5520, Wescor, Logan, UT, USA). Osmotic potential (π_{osm}) given by the osmometer was

248 used to estimate (π_{tlp}) using the equation $\pi_{tlp} = 0.832\pi_{osm}^{-0.631}$ (Bartlett et al., 2012).

249 *Statistical Analysis*

250 For each drought year, we calculated metrics of drought resistance (Rt), recovery (Rc), and resilience (Rs),

251 following Lloret et al. (2011) (Table 3). We defined Rt as the ratio of basal area increment (BAI; *i.e.*,

252 change in cross-sectional area) during the drought year to the mean BAI over the five years preceding the

253 drought. Rc was defined as the ratio of mean BAI over the five years following the drought to BAI of the

254 drought year. Rs was defined as the ratio of mean BAI over the five years following the drought to that of

255 the five years preceding the drought. Thus, for all metrics, values <1 and >1 indicate growth reductions and

256 increases, respectively.

257 Because these metric could potentially be biased by directional pre-drought growth trends, we also tried an

258 intervention time series analysis (ARIMA, Hyndman et al., 2020) that predicted mean drought-year growth

259 based on trends over the preceding ten years and used this value in place of the five-year mean in calculations

260 of resistance (Rt_{ARIMA}= observed BAI/ predicted BAI). Rt and Rt_{ARIMA} were strongly correlated (Fig.

261 **S5**), and showed similar responses to the independent variables of interest (cf. Tables S4-55, S8-S9). Visual

262 review of the individual tree-ring sequences with the largest discrepancies between these metrics revealed

263 that Rt was less prone to unreasonable estimates than Rt_{ARIMA}. We therefore determined that use of 5-year

264 means, as described above, were more appropriate metrics than those based on ARIMA projections.

265 Analyses focused on testing the predictions presented in Table 1 with Rt (or Rt_{ARIMA}), Rc, or Rs as the

266 response variable. Models were run for all drought years combined and for each drought year individually.

267 The general statistical model for hypothesis testing was a mixed effects model, implemented in the lme4

268 package in R (Bates et al., 2019). In the multi-year model, we included a random effect of tree nested within

269 species and a fixed effect of drought year to represent the combined effects of differences in drought

270 characteristics. Individual year models included a random effect of species. All models included fixed effects

271 of independent variables of interest (Tables 1,3) as specified below. All variables across all best models had

272 variance inflation factors <1.2 (1 +/- 0.019). We used Akaike information criterion with correction for small

273 sample sizes (AICc; see Brewer et al., 2016) to assess model selection, and conditional/marginal R-squared to

274 assess model fit as implemented in the AICcmodavg package in R (Mazerolle and portions of code

275 contributed by Dan Linden., 2019). Individual model terms were considered significant when their addition

276 to a model improved fit at ΔAICc $\geq$ 2.0, where ΔAICc is the difference in AICc between models with and

277 without the trait.

278 To avoid over-fitting models with five species traits (Table 3) across only 12 species, we did not include all

279 traits as fixed effects in a single linear mixed model, but rather conducted individual tests of each species

280 trait to determine the relative importance and appropriateness for inclusion in the main model. These tests

281 followed the model structure specified above, then added $ln[H]$ and $ln[TWI]$ to create a base model against

282 which we tested traits. Trait variables were considered appropriate for inclusion in the main model if their

283 addition to the base model significantly improved fit for at least one metric of drought tolerance (Rt, Rc, or

284 Rs; Tables S4,S6-S7). While we tested xylem porosity as a predictor (Table 1), we did not consider it

285 appropriate for inclusion in the main model because of highly uneven distribution of species across categories

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286 (Table 2) and opposite drought responses of the only two diffuse-porous species (detailed below).

287 We then determined the top full models for predicting each dependent variable. To do so, we compared
288 models with all possible combinations of candidate variables, including $ln[H]*ln[TWI]$ and species traits as
289 specified above. We identified the full set of models within ΔAICc=2 of the best model (that with lowest
290 AICc). When a variable appeared in all of these models and the sign of the coefficient was consistent across
291 models, we viewed this as support for the acceptance/rejection of the associated prediction (Table 1). If the
292 variable appeared in some but not all of these models, and its sign was consistent across models, we
293 considered this partial support/rejection.

294 All analysis beyond basic data collection was performed using R version 3.6.2 (R Core Team, 2019). Other
295 R-packages used in analyses are listed in the Supplementary Information (Appendix S1). All data, code, and
296 results are available through the SCBI-ForestGEO organization on GitHub
297 (https://github.com/SCBI-ForestGEO: SCBI-ForestGEO-Data and McGregor_climate-sensitivity-variation
298 repositories), with static versions corresponding to data and analyses presented here archived in Zenodo
299 (DOIs: 10.5281/zenodo.3604993 and *[TBD]*, respectively.

Results

Tree height and microenvironment

302 In the years for which we have vertical profiles in climate data (2016-2018), taller trees–or those in dominant
303 crown positions– were generally exposed to higher evaporative demand during the peak growing season
304 months (May-August; Fig. **2**). Specifically, maximum daily wind speeds were significantly higher above the
305 top of the canopy (40-50m) than within and below (10-30m) (Fig. **2a**). Relative humidity was also somewhat
306 lower during June-August, ranging from ~50-80% above the canopy and ~60-90% in the understory (Fig. **2b**).
307 Air temperature did not vary consistently across the vertical profile (Fig. **2c**).

308 Crown position varied as expected with height (dominant > co-dominant > intermediate > suppressed), but
309 with substantial variation (Fig. **2d**). There were significant differences in height across all crown position
310 classes (Fig. **2d**). A comparison test between height and crown position data from the most recent
311 ForestGEO census (2018) revealed a correlation of 0.73.

Community-level drought responses

313 At the community level, cored trees showed substantial growth reductions in all three droughts, with a mean
314 Rt of 0.86 in 1966 and 1999, and 0.84 in 1977 (Fig. **1b**). Across the entire study period (1950-2009), the
315 focal drought years were the three years with the largest fraction of trees exhibiting $Rt \leq 0.7$. Specifically, in
316 each drought, roughly 30% of the cored trees had growth reductions of $\geq 30\%$ ($Rt \leq 0.7$): 29% in 1966, 32%
317 in 1977, and 27% in 1999. However, some individuals exhibited increased growth, *i.e.*, $Rt > 1.0$: 26% of trees
318 in 1966, 22% in 1977, and 26% in 1999. Recovery was generally strong and complete, with Rc averaging 1.55
319 in 1966, 1.42 in 1977, and 1.34 in 1999 (Fig. **S6**) and Rs averaging 1.28 in 1966, 1.19 in 1977, and 1.12 in
320 1999 (Fig. **1c**).

321 In the context of the multivariate model, Rt did not vary across drought years. That is, drought year as a
322 variable did not appear in any of the top models – *i.e.*, models that were statistically indistinguishable
323 (ΔAICc<2) from the best model (see footnotes on Tables S8-S9). In contrast, both Rc and Rs varied across
324 years, being highest in all of the top models (Tables S10-S11), in which both were highest in 1966,

325 intermediate in 1977, and lowest in 1999.

326 *Tree height, microenvironment, and drought tolerance*

327 Taller trees (based on H in the drought year) showed stronger growth reductions during drought (i.e., lower
328 Rt) and less resilience following drought (i.e., lower Rc and Rs; Table 1; Fig. **4**). Specifically, for Rt, $ln[H]$
329 appeared, with negative coefficient, in the best model (ΔAICc=0) and all top models when evaluating the
330 three drought years together (Tables S8-S9). The same held true for 1966 individually, but there was no
331 significant effect of $ln[H]$ for 1977 or 1999 individually. For Rc, $ln[H]$ appeared, with negative coefficient, in
332 the best model without a $ln[H] * ln[TWI]$ interaction, for the three drought years together and for 1977, but
333 not for 1966 or 1999. For Rs, again considering the best models without a $ln[H] * ln[TWI]$ interaction, there
334 was a negative effect of $ln[H]$ for the three drought years together and for 1966 and 1977, and a
335 non-significant negative trend in 1999.

336 Trees in drier microsites showed greater growth declines during drought; i.e., Rt had a significantly negative
337 response to $ln[TWI]$ across all drought years combined, and in 1977 and 1999 individually (Fig. **4**, Table
338 S8-S9). The $ln[H] * ln[TWI]$ interaction was never significant, and had a positive sign in any top Rt models
339 in which it appeared (Tables 1, S8-S9), rejecting the hypothesis that smaller trees (presumably with smaller
340 rooting volume) are more susceptible to drought in microenvironments with a deeper water table. In
341 contrast, $ln[TWI]$ did not appear in any of the best models for Rc or Rs (combined of for individual years),
342 except in interaction with $ln[H]$ (Fig. 4, Tables S10-S11). Negative $ln[H] * ln[TWI]$ interactions appeared in
343 the best models for both Rc and Rs for all years combined, as well as in one individual year for each (1966
344 for Rc, 1977 for Rs). This implies that small trees had greater recovery and resilience in wetter
345 microhabitats, whereas large trees had greater recovery and resilience in dry microhabitats.

346 *Species' traits and drought tolerance*

347 Species, as a factor in ANOVA, had significant influence (p<0.05) on all traits (wood density, LMA, PLA_{dry},
348 and π_{tlp}), with more significant pairwise differences for wood density and PLA_{dry} than for LMA and π_{tlp}
349 (Table 2, Fig. **S4** as characterized by the agricolae package de Mendiburu (2020)). Drought tolerance also
350 varied across species, overall and in each drought year (Figs. **3, S7**). Species with overall lowest and highest
351 Rt and Rs were, respectively, *Liriodendron tulipifera* (mean Rt = 0.66, mean Rs = 1.04) and *Fagus*
352 *grandifolia* (mean Rt = 0.99; mean Rs = 1.65). These two species–notably the only two diffuse-porous
353 species in our study–differed significantly from one another in Rt and Rs in each drought year (Fig. **3**).

354 Wood density, LMA, and xylem porosity were all poor predictors of drought tolerance (Tables 1,S4-S5).
355 Wood density and LMA were never significantly associated with Rt, Rc, or Rs in the single-variable tests
356 and were therefore excluded from the full models. Xylem porosity had no significant influence on Rt or Rs in
357 models for all droughts combined (Tables S4, S7). In contrast, Rc was significantly higher in diffuse- and
358 semi-ring porous species than in ring-porous species (Table S6, Fig. 3).

359 Drought resistance and resilience, but not recovery, were negatively correlated with PLA_{dry} and π_{tlp} (Fig. **4**;
360 Tables 1, S4-S11). For Rt, PLA_{dry} had a significant influence, with negative coefficient, in top models for the
361 three droughts combined and for the 1966 drought individually (Fig. **4**; Tables S8-S9). It was also included
362 in some of the top models for 1999 (Tables S8-S9). π_{tlp} was included with a negative coefficient in the best
363 model for both all droughts combined and for the 1977 drought individually (Fig. **4**; Table S8), although its
364 influence was not significant at ΔAICc<2. It was also included in some of the top models for 1999 (Tables

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365 S8-S9).

366 Recovery was not significantly correlated with either PLA_{dry} or π_{tlp}. There was only one best Rc model
367 containing one of these terms (π_{tlp} in 1977 drought), but in no instance was one of these terms included in
368 all top models (i.e., at ΔAICc<2).

369 For Rs, PLA_{dry} was in the best models for the three droughts combined and for the 1966 drought
370 individually, and some of the top models for 1977 and 1999 (Fig. **4**; Table S11); however, its effects were not
371 significant atat ΔAICc<2. π_{tlp} was in the best models for the three droughts combined and for 1966 and
372 1999 individually, and in one of the top models for 1977 (Fig. **4**; Table S11). It's effects were significant at
373 ΔAICc<2 for 1999 only.

Discussion

375 Tree height, microenvironment, and leaf drought tolerance traits shaped tree growth responses across three
376 droughts at our study site (Table 1, Fig. **4**). The greater susceptibility of larger trees to drought, similar to
377 forests worldwide (Bennett et al., 2015), was driven primarily by their height (Stovall et al., 2019). Taller
378 height was likely a liability in itself, and was also associated with greater exposure to conditions that would
379 promote water loss and heat damage during drought (Fig. **2**). There was no evidence that greater
380 availability of, or access to, soil water availability increased drought resistance; in contrast, trees in wetter
381 topographic positions had lower Rt (Zuleta et al., 2017; Stovall et al., 2019), and the larger potential rooting
382 volume of large trees provided no advantage in the drier microenvironments. The negative effect of height on
383 Rt held after accounting for species' traits, which is consistent with recent work finding height had a stronger
384 influence on mortality risk than forest type during drought (Stovall et al., 2020). Drought tolerance was not
385 consistently linked to species' LMA, wood density, or xylem type (ring- vs. diffuse porous), but was
386 negatively correlated with leaf drought tolerance traits (PLA_{dry}, π_{tlp}). This is the first study to our
387 knowledge linking PLA_{dry} and π_{tlp} to growth reduction during drought. The directions of these responses
388 were consistent across droughts (Table S8), supporting the premise that they were driven by fundamental
389 physiological mechanisms. However, the strengths of each predictor varied across droughts (Fig. **4**; Tables
390 S8-S9), indicating that drought characteristics interact with tree size, microenvironment, and traits to shape
391 which individuals are most affected. These findings advance our knowledge of the factors that make trees
392 vulnerable to stem growth declines during drought and, by extension, likely make them more vulnerable to
393 mortality (Sapes et al., 2019).

394 The droughts considered here were of a magnitude that has occurred with an average frequency of
395 approximately once every 10-15 years (Fig. **1a**, Helcoski et al., 2019) and had substantial but not
396 devastating impacts on tree growth (Figs. **1b**). These droughts were classified as severe ($PDSI$ < -3.0; 1977)
397 or extreme ($PDSI$ < -4.0; 1966, 1999) at our site and have been linked to tree mortality in the eastern
398 United States (Druckenbrod et al., 2019). However, extreme, multiannual droughts such as the so-called
399 "megadroughts" of this type that have triggered massive tree die-off in other regions (e.g., Allen et al., 2010;
400 Stovall et al., 2019) have not occurred in the Eastern United States within the past several decades (Clark
401 et al., 2016). Of the droughts considered here, the 1966 drought, which was preceded by two years of dry
402 conditions (Fig. **S1**), severely stressed a larger portion of trees (Fig. **1b**). The tendency for large trees to
403 have lowest resistance was most pronounced in this drought, consistent with other findings that this
404 physiological response increases with drought severity (Bennett et al., 2015; Stovall et al., 2019). Across all
405 three droughts, the majority of trees experienced reduced growth, but a substantial portion (e.g., short

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understory trees, species with drought resistant traits; Fig. **4**) had increased growth (Fig. **1b**), consistent with prior observations that smaller trees can exhibit increased growth rates during drought (Bennett et al., 2015). It is likely because of the moderate impact of these droughts, along with other factors influencing tree growth (e.g., stand dynamics), that our best models characterize only a modest amount of variation in Rt: 11-12% for all droughts combined, and 18-25% for each individual drought (Table S8).

Consistent with studies in other forests worldwide (Bennett et al., 2015), taller trees in this forest exhibited lower drought resistance–*and also recovery and resilience.* Mechanistically, this is consistent with, and reinforces, previous findings that it impossible for trees to efficiently transport water to great heights and simultaneously maintain strong resistance and resilience to drought-induced embolism (Olson et al., 2018; Couvreur et al., 2018; Roskilly et al., 2019). Taller trees also face dramatically different microenvironments (Fig. **2**). They are exposed to higher wind speeds and lower humidity (Fig. **2a-b**), resulting in higher evaporative demand. Unlike other temperate forests where modestly cooler understory conditions have been documented (Zellweger et al., 2019), particularly under drier conditions (Davis et al., 2019), we observed no significant variation in air temperatures across the vertical profile (Fig. **2c**). More critically for tree physiology, leaf temperatures can become significantly elevated over air temperature under conditions of high solar radiation and low stomatal conductance (Campbell and Norman, 1998; Rey-Sánchez et al., 2016). Under drought, when air temperatures tend to be warmer, direct solar radiation tends to be higher (because of less cloud cover), and less water is available for evaporative cooling of the leaves, trees with sun-exposed crowns may not be able to simultaneously maintain leaf temperatures below damaging extremes and avoid drought-induced embolism. Indeed, previous studies have shown lower drought resistance in more exposed trees (Liu and Muller, 1993; Suarez et al., 2004; Scharnweber et al., 2019). Unfortunately, collinearity between height and crown exposure in this study (Fig. **2d**) makes it impossible to confidently partition causality. Additional research comparing drought responses of early successional and mature forest stands, along with short and tall isolated trees, would be valuable for more clearly disentangling the roles of tree height and crown exposure.

Belowground, taller trees would tend to have larger root systems (Enquist and Niklas, 2002; Hui et al., 2014), but this does not necessarily imply that they have greater access to or reliance on deep soil-water resources that may be critical during drought. While tree size can correlate with the depth of water extraction (Brum et al., 2019), the linkage is not consistent. Shorter trees can vary broadly in the depth of water uptake (Stahl et al., 2013), and larger trees may allocate more to abundant shallow roots that are beneficial for taking up water from rainstorms (Meinzer et al., 1999). Moreover, reliance on deep soil-water resources can actually prove a liability during severe and prolonged drought, as these can experience more intense water scarcity relative to non-drought conditions (Chitra-Tarak et al., 2018). In any case, the potentially greater access to water did not override the disadvantage conferred by height–and, in fact, greater moisture access in non-drought years (here, higher TWI) appears to make trees more sensitive to drought (Zuleta et al., 2017; Stovall et al., 2019). This may be because moister habitats would tend to support species and individuals with more mesophytic traits (Bartlett et al., 2016b; Mencuccini, 2003; Medeiros et al., 2019), potentially growing to greater heights [e.g., Detto et al. (2013), and these are then more vulnerable when drought hits. The observed height-sensitivity of Rt, together with the lack of conferred advantage to large stature in drier topographic positions, agrees with the concept that physiological limitations to transpiration under drought shift from soil water availability to the plant-atmosphere interface as forests age (Bretfeld et al., 2018), such that tall, dominant trees are the most sensitive in mature forests. Again, additional research comparing

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drought responses across forests with different tree heights and water availability would be valuable for disentangling the relative importance of above- and belowground mechanisms across trees of different size.

The development of tree-ring chronologies for the twelve most dominant tree species at our site (Helcoski et al., 2019; Bourg et al., 2013) gave us the sample size to compare historical drought responses across species (Fig. **3**) and associated traits at a single site (see also Elliott et al., 2015). Our study reinforced current understanding (see Introduction) that wood density and LMA are not reliably linked to drought resistance (Table 1). Contrary to several previous studies in temperate deciduous forests (Friedrichs et al., 2009; Elliott et al., 2015; Kannenberg et al., 2019), we did not find an association between xylem porosity and drought resistance, as the two diffuse-porous species, *Liriodendron tulipifera* and *Fagus grandifolia*, were at opposite ends of the Rt spectrum (Fig. **3**). While the low Rt of *L. tulipifera* is consistent with other studies (Elliott et al., 2015), the high Rt of *F. grandifolia* contrasts with studies identifying diffuse porous species in general (Elliott et al., 2015; Kannenberg et al., 2019), and the genus *Fagus* in particular (Friedrichs et al., 2009), as drought sensitive. There are two potential explanations for this discrepancy. First, other traits can and do override the influence of xylem porosity on drought resistance. Ring-porous species are restricted mainly to temperate deciduous forests, while highly drought-tolerant diffuse-porous species exist in other biomes (Wheeler et al., 2007). *Fagus grandifolia* had intermediate π_{tlp} and low PLA_{dry} (Fig. **S4**), which would have contributed to its drought resistance (Fig. **4**; see discussion below). A second explanation of why *F. grandifolia* trees at this particular site had higher Rt is that the sampled individuals, reflective of the population within the plot, are generally shorter and in less-dominant canopy positions compared to most other species (Fig. **S4**). The species, which is highly shade-tolerant, also has deep crowns (Anderson-Teixeira et al., 2015b), implying that a lower proportion of leaves would be affected by harsher microclimatic conditions at the top of the canopy under drought (Fig. **2**). Thus, the high Rt of the sampled *F. grandifolia* population can be explained by a combination of fairly drought-resistant leaf traits, shorter stature, and a buffered microenvironment.

Concerted measurement of tree-rings and leaf drought tolerance traits of emerging importance (Scoffoni et al., 2014; Bartlett et al., 2016a; Medeiros et al., 2019) allowed novel insights into the role of drought tolerance traits in shaping drought response. The finding that PLA_{dry} and π_{tlp} can be useful for predicting drought responses of tree growth (Fig. **4**; Table 1) is both novel and consistent with previous studies linking these traits to habitat and drought tolerance. Previous studies have demonstrated that π_{tlp} and PLA_{dry} are physiologically meaningful traits linked to species distribution along moisture gradients (Maréchaux et al., 2015; Fletcher et al., 2018; Medeiros et al., 2019; Simeone et al., 2019; Rosas et al., 2019; Zhu et al., 2018), and our findings indicate that these traits also influence drought responses. Furthermore, the observed linkage of π_{tlp} to Rt in this forest aligns with observations in the Amazon that π_{tlp} is higher in drought-intolerant than drought-tolerant plant functional type. Further, it adds support to the idea that this trait is useful for categorizing and representing species' drought responses in models (Powell et al., 2017). Because both PLA_{dry} and π_{tlp} can be measured relatively easily (Bartlett et al., 2012; Scoffoni et al., 2014), they hold promise for predicting drought growth responses across diverse forests. The importance of predicting drought responses from species traits increases with tree species diversity; whereas it is feasible to study drought responses for all dominant species in most boreal and temperate forests (e.g., this study), this becomes difficult to impossible for species that do not form annual rings, and for diverse tropical forests. Although progress is being made for the tropics (Schöngart et al., 2017), a full linkage of drought tolerance traits to drought responses would be invaluable for forecasting how little-known species and whole forests will

respond to future droughts (Christoffersen et al., 2016; Powell et al., 2017).

As climate change drives increasing drought in many of the world's forests (Trenberth et al., 2014; Intergovernmental Panel on Climate Change, 2015), the fate of forests and their climate feedbacks will be shaped by the biophysical and physiological drivers observed here. Our results show that taller, more exposed trees and species with less drought-tolerant leaf traits will be most affected in terms of growth during the drought year. Survival is linked to resistance and resilience [**CHECK REFS**] (DeSoto et al., 2020; Gessler et al., 2020), implying it may be influenced by the same factors. Indeed, while the influence of PLA_{dry} and π_{tlp} on drought survival remains to be tested, taller trees have lower survival (Bennett et al., 2015; Stovall et al., 2019). As climate change-driven droughts affect forests worldwide, there is likely to be a shift from mature forests with tall, buffering trees to forests with a shorter overall stature (McDowell et al., 2020). At this point, species whose drought tolerance relies in part on existence within a buffered microenvironment (e.g., *F. grandifolia*) could in turn become more susceptible. Here, the relative importance of tree height *per se* versus crown exposure becomes crucial, shaping whether the dominant trees of shorter canopies are significantly more drought tolerant because of their shorter stature, or whether high exposure makes them as vulnerable as the taller trees of the former canopy. Studies disentangling the influence of height and exposure on drought tolerance will be critical to answering this question. Ultimately, distributions of tree heights and drought tolerance traits across broad moisture gradients suggest that forests exposed to more drought will shift towards shorter stature and be dominated by species with more drought-tolerant traits (Liu et al., 2019; Bartlett et al., 2016a; Zhu et al., 2018). Our study helps to elucidate the mechanisms behind these patterns, opening the door for more accurate forecasting of forest responses to future drought.

Author Contribution

KAT, IM, and AJT designed the research. Tree-ring chronologies were developed by RH under guidance of AJT and NP. Trait data were collected by IM, JZ under guidance of NK and LS. Other plot data were collected by IM, AS, EGA, and NB under guidance of EGA and WM. Data analyses were performed by IM under guidance of KAT and VH. KAT and IM interpreted the results. IM and KAT wrote the first draft of manuscript, and all authors contributed to revisions.

Supplementary Information

NEED TO UPDATE !!** Table S1. Monthly Palmer Drought Severity Index (PDSI), and its rank among all years between 1950 and 2009 (driest=1), for focal droughts.

Table S2. Species-specific bark thickness regression equations.

Table S3. Species-specific height regression equations.

Table S4. Individual tests of species traits as drivers of drought resistance, where Rt is used as the response variable.

Table S5. Individual tests of species traits as drivers of drought resistance, where Rt_{ARIMA} is used as the response variable.

Table S6. Summary of top full models for each drought instance, where Rt is used as the response variable.

Table S7. Summary of top models for each drought instance, where Rt_{ARIMA} is used as the response variable.

Figure S1. Time series of Palmer Drought Severity Index (PDSI) for the 2.5 years prior to each focal drought

Figure S2. Map of ForestGEO plot showing topographic wetness index and location of cored trees

Figure S3. Distribution of reconstructed tree heights across drought years.

Figure S4. Distribution of independent variables by species.

Figure S5. Comparison of Rt and Rt_{ARIMA} results, with residuals, for each drought scenario

Figure S6. Visualization of best model, with data, for all droughts combined.

Appendix S1. Further Package Citations

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